

A REVIEW OF THE GENUS *HYPOTHYRIS* HÜBNER
(NYMPHALIDAE), WITH DESCRIPTIONS OF
THREE NEW SUBSPECIES AND EARLY
STAGES OF *H. DAPHNIS*¹

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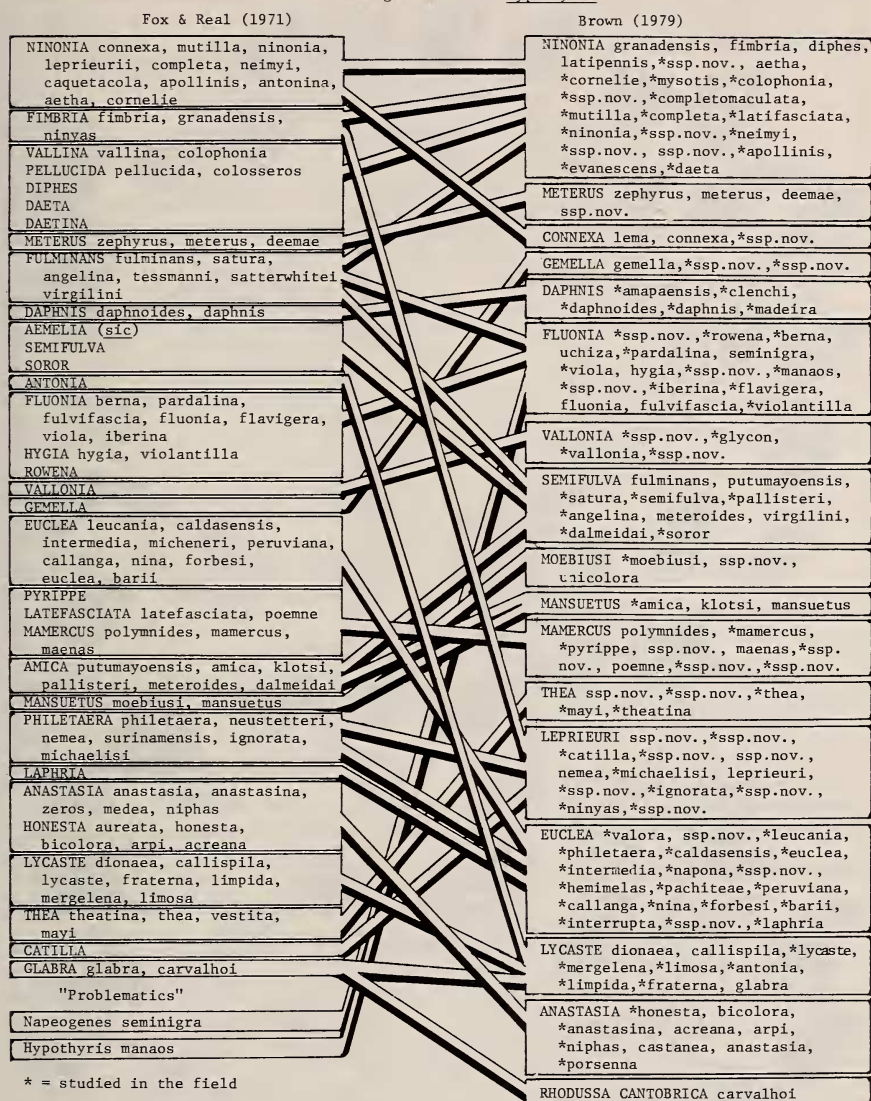
ABSTRACT. The Neotropical genus *Hypothyris* (Lepidoptera: Nymphalidae: Ithomiinae: Napeogenini) is regarded on biosystematic grounds, as including 16 species divided into 137 geographical subspecies (34 still undescribed). The distributions of *Hypothyris* subspecies have been used to help define centers of butterfly endemism (at the lowest recognized taxonomic level) in the Neotropical forests; these correlate well with areas of high probability for forest continuity during the cool-dry spell at the end of the Würm-Wisconsin glaciation, 13,000-20,000 years ago. Three new subspecies described for the little-known *H. daphnis* D'Almeida extend its range to Amapá, extreme northwestern Pará, southern Maranhão, and the lower Rio Madeira. The early stages of the new subspecies from Amapá (illustrated) are similar to those of other solitary-feeding species of *Hypothyris*.

Fox & Real (1971) revised the Neotropical genus *Hypothyris* Hübner (Napeogenini). This revision was concluded under extenuating circumstances, after the death of the senior author and with limited access to important type material in British and continental museums; nevertheless, it was a major step in understanding the systematics of these mimetic butterflies.

Recent fieldwork in the Neotropics and visits to the British Museum (Natural History) led to a new revision of the biosystematics of the genus and the relation of natural biogeographical units to taxonomic names. This work was presented as a preliminary reorganization of Fox and Real's order for the genus (Brown, 1977). This supplementary revision has now been further refined (Brown, 1979; Mielke and Brown, 1979) by additional field and museum study, especially the examination of Haensch and Weymer types in the Museum für Naturkunde (Humboldt-Universität, Berlin). The new biosystematic vision of this complex genus, including 16 species and 137 subspecies (34 of them undescribed), is supported by morphological studies and the discovery of intergrading populations in narrow hybridization zones between subspecies (Figs. 1-12; Appendix). Final definition of this genus and of other genera in the tribe will only be possible,

¹The Ithomiines of Brazil (Lepidoptera: Nymphalidae), Part VI; and Geographical Patterns of Evolution in Neotropical Lepidoptera, Part VII. For previous parts, See Brown (1977, 1979). Dedicated to the memories of Richard M. Fox and Harry K. Clench, who stimulated and assisted this research during the author's visits to the Carnegie Museum.

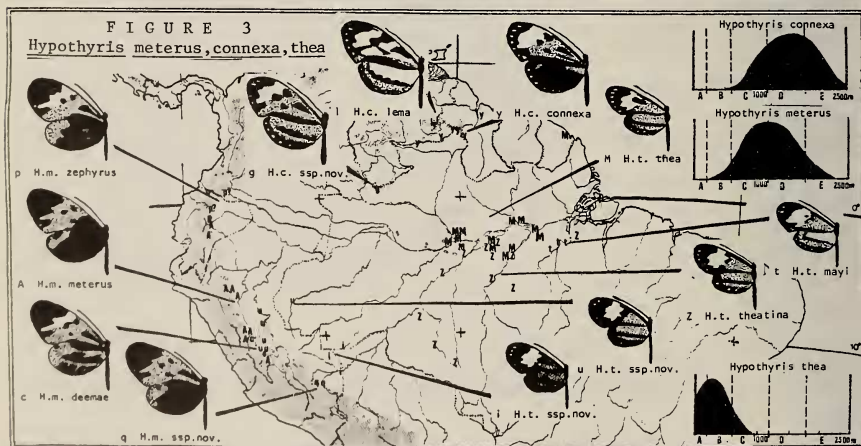
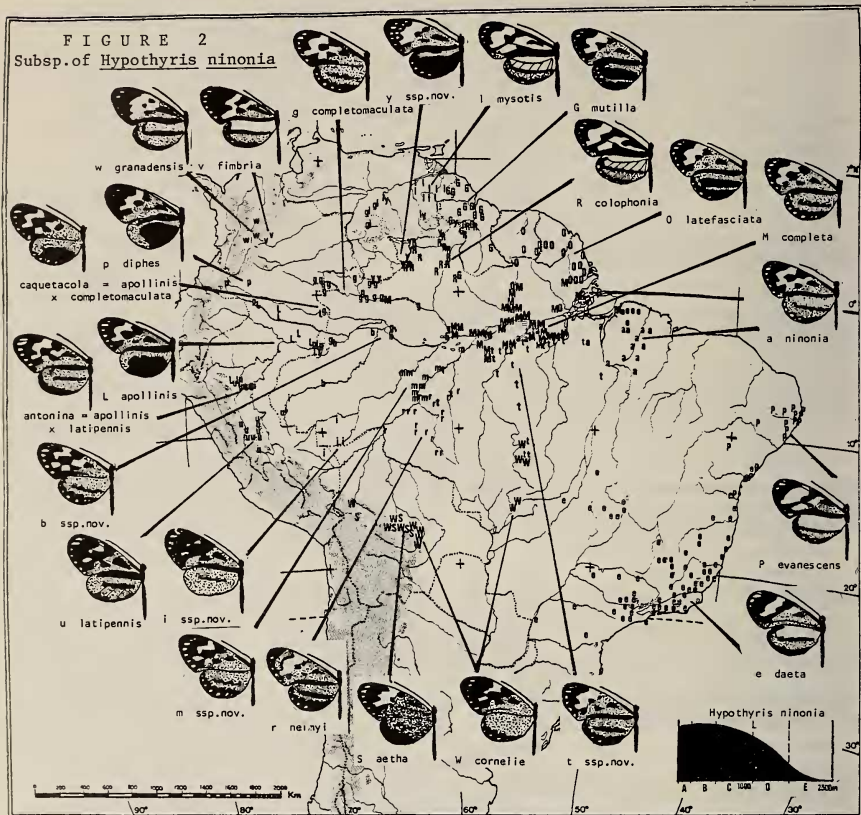
FIGURE 1: Reorganization of *Hypothyris*

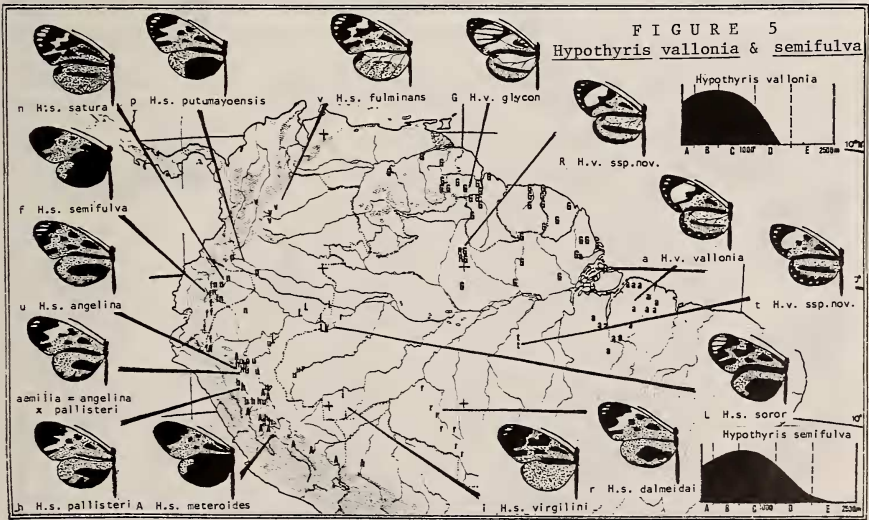
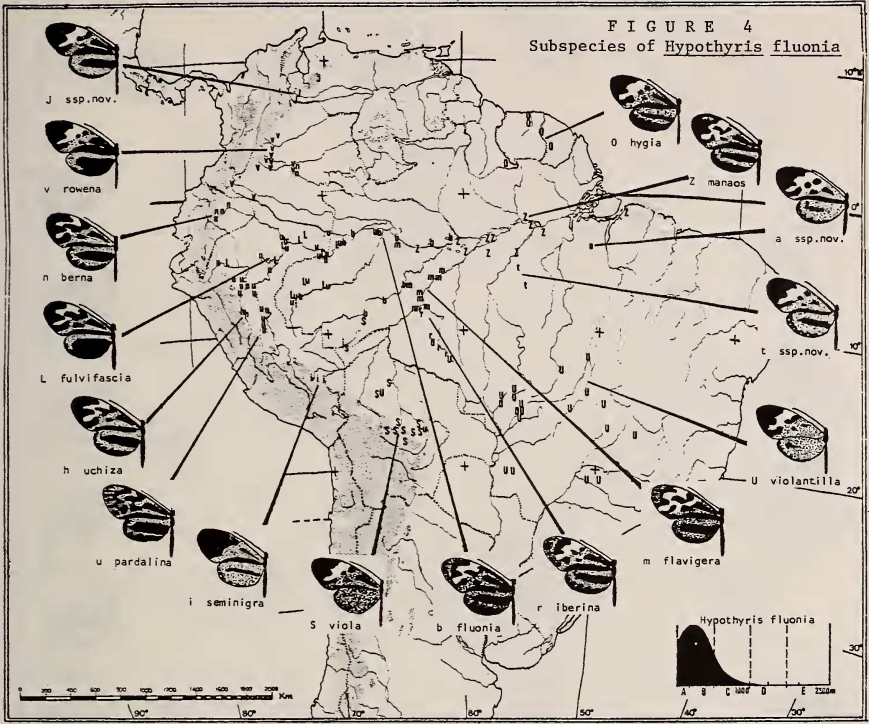


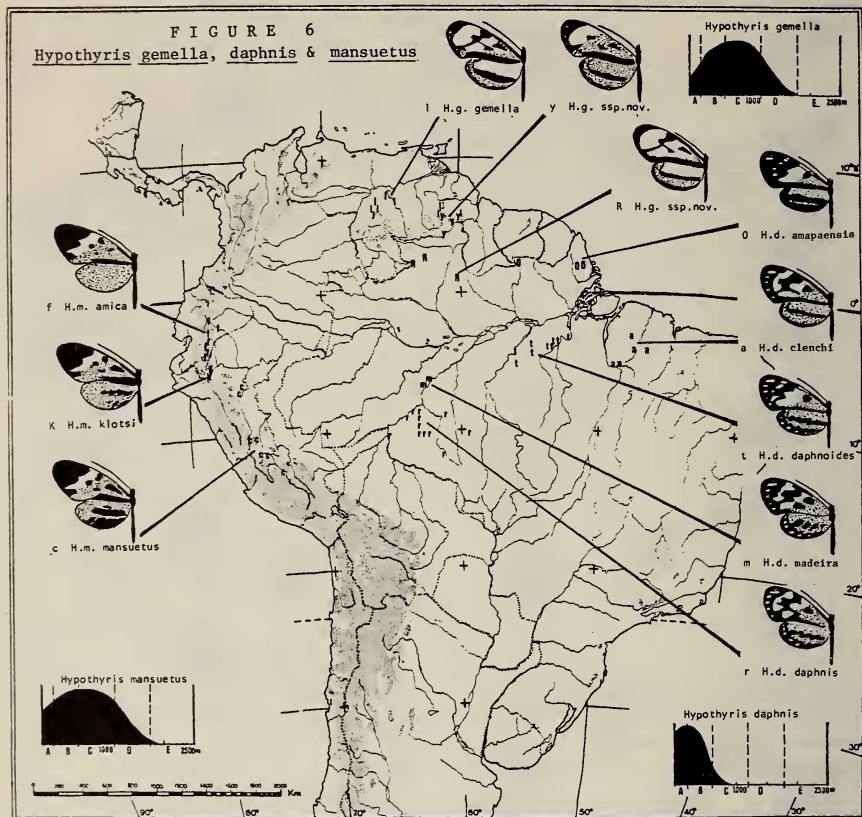
* = studied in the field

however, after extensive additional biological work and experimentation.

The genus *Hypothyris* was among the most useful in the isoline determination of endemic centers for butterfly subspecies in the Neotropical forests (Brown, 1979, 1980; see Fig. 13). Of the 62 discrete







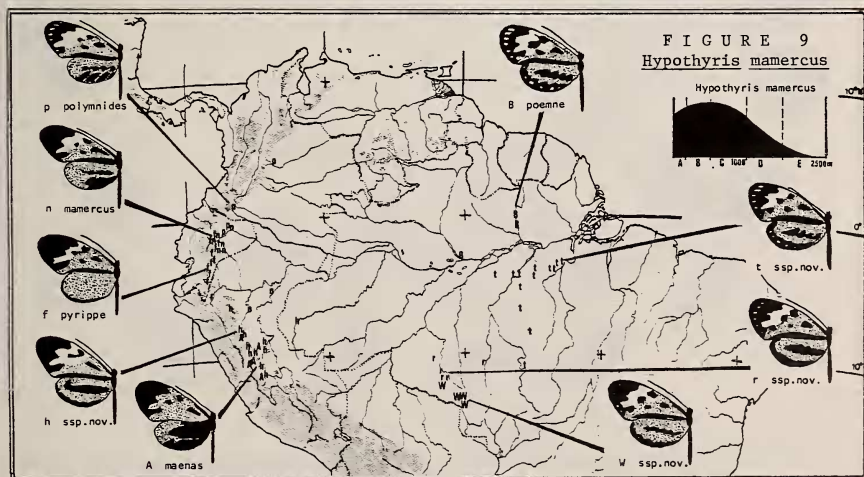
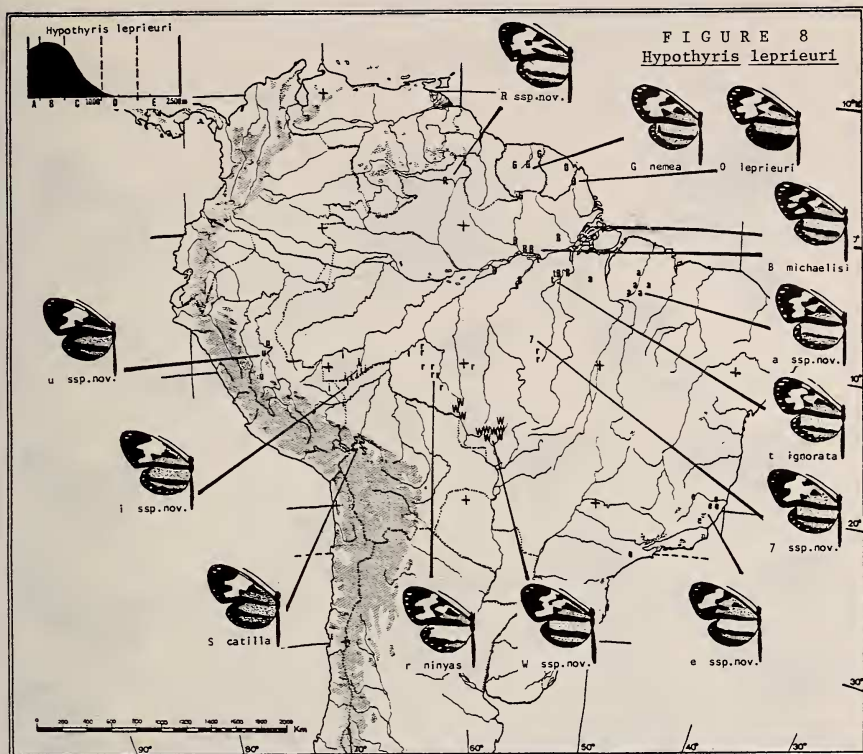
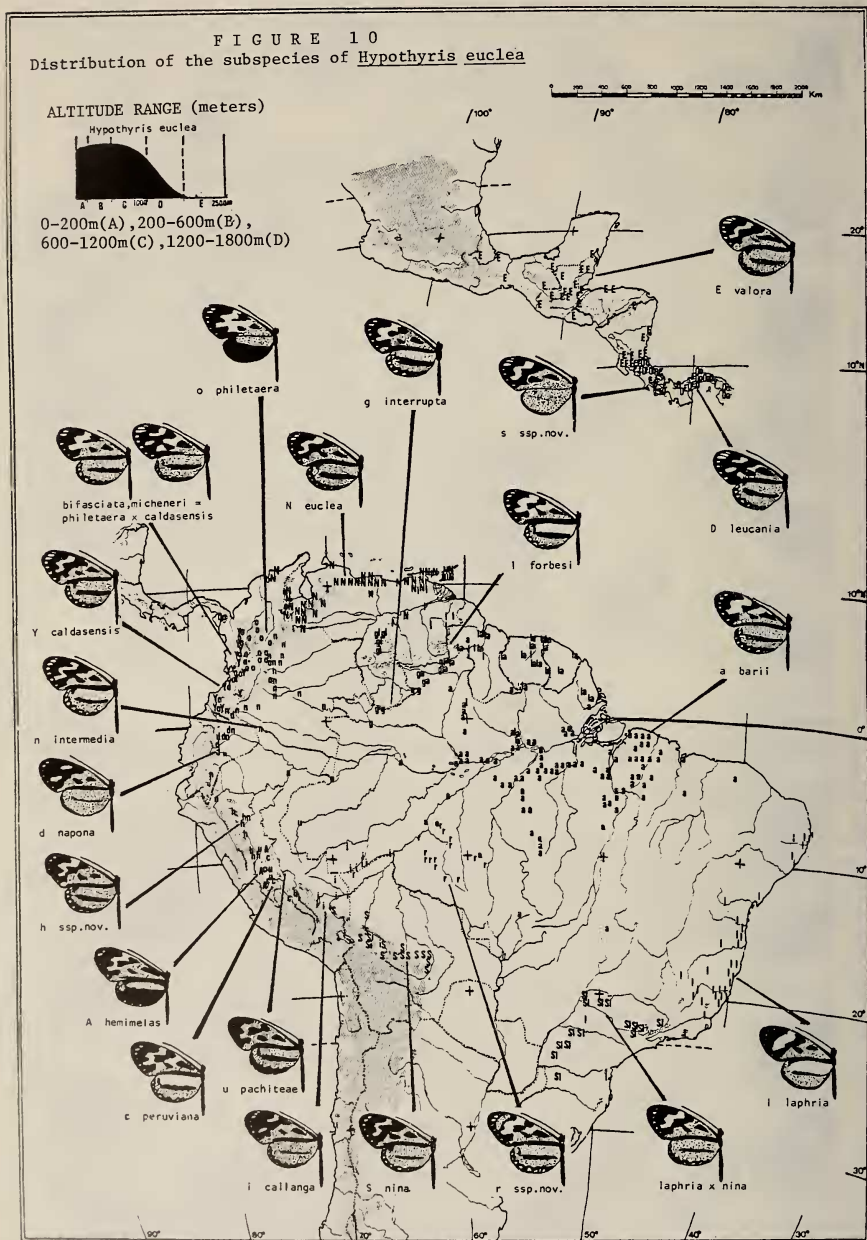
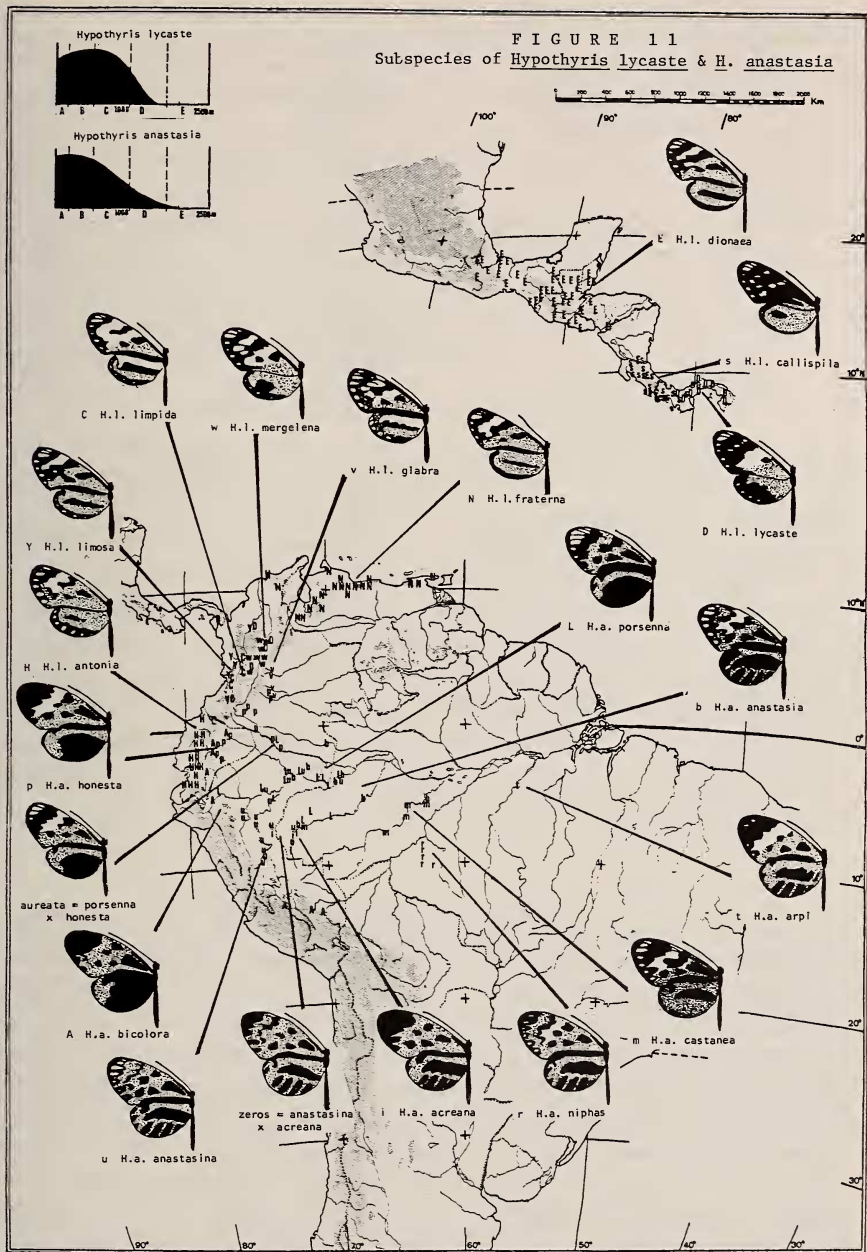


FIGURE 10

Distribution of the subspecies of *Hypothesis euclea*



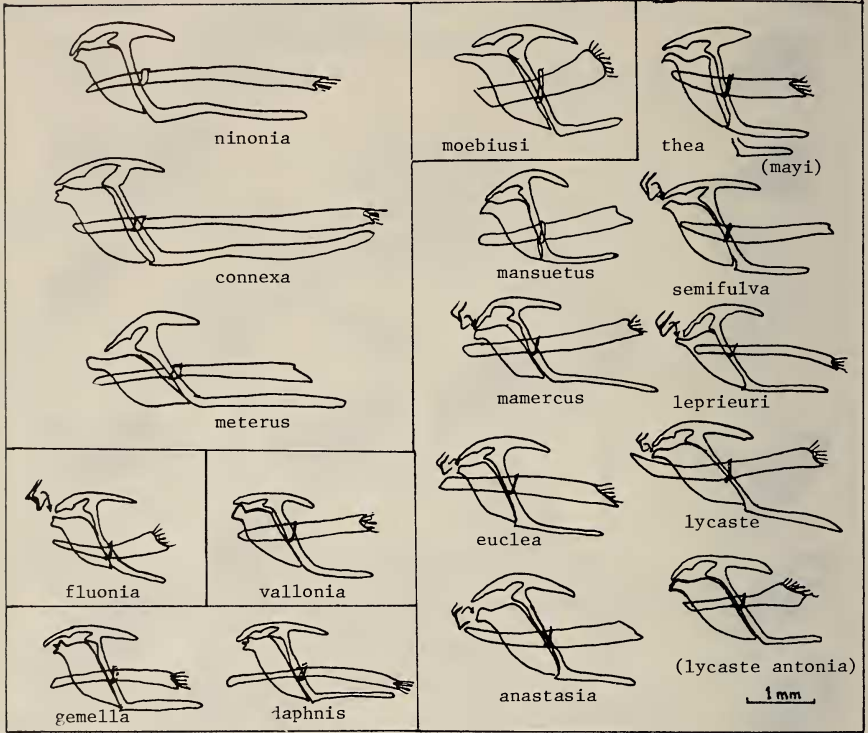


FIG. 12. Male genital armatures of *Hypothyris* species, right side, with details of valve tip (from above) when important; schematic.

areas predicted by geoscientific evidence to represent regions of high probability for longterm forest stability through the major climatic variations of the late Pleistocene (Fig. 14), all but 10 corresponded to regional subspeciation patterns in a majority of local sets of the 123 species (and 867 subspecies) of Heliconiini and Ithomiinae analyzed (Brown, 1979: 146B). Of the 44 major endemic centers recognized for this set of butterfly subspecies, 38 could be seen in those of the genus *Hypothyris* (Appendix). It is hoped that this "palaeoecological forest refuge model" (Fig. 14) may be evaluated by the examination of regional subspeciation patterns in a variety of groups of Neotropical forest Lepidoptera. Most of the centers of endemism detected in the Heliconiini and Ithomiinae (which correlate well with the regions of high probability for stability in the geoscientific model) have also been seen in a variety of other sedentary forest butterfly groups ex-

amed at the level of regional subspecies (Morphinae, Brassolini, *Phyciodes sensu lato*, Callicorini, Charaxinae, Troidini, Dismorphinae, and a variety of Lycaenidae and Hesperioidea), as the model would predict. Note, however, that the model does not relate to species biogeography (since many butterfly species pre-date the Pleistocene), nor to local species diversity (which is usually determined by parameters of the physical environment that set a limit on packing of the species potentially present). Indeed, many of the subspecies hybridization quadrants (black in Fig. 13) show exceptionally high species diversity, and are often the source of many dispersive and weedy "commercial" Lepidoptera.

SUBSPECIES AND BIOLOGY OF *HYPOTHYRIS DAPHNIS*

By far the least known species in the genus *Hypothyris* is *H. daphnis* D'Almeida (Figs. 6, 15–21). Two of the subspecies, *H. d. daphnis* and *H. d. daphnoides*, were described only recently (1945). Three additional subspecies have come to light in the past six years, extending the continuous range of this characteristic species to the limits of the Amazon forest in Brazil, east of the basins of the Rios Madeira and Cuminá. The early stages of one of these new subspecies were observed in central Amapá in mid-1978, and are described briefly here. The three new subspecies also are described. Material is distributed to museums in which *H. daphnis* is poorly or not represented.

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FIG. 13. Centers of butterfly subspecies endemism in the Neotropical forests (Brown, 1979, 1980), based on 3500 localities, 1520 quadrants (of 30' × 30' latitude and longitude), and quadrant lists for 123 species and 867 subspecies of forest Heliconiini and Ithomiinae (including all the *Hypothyris*). A double correction is applied for hybridization of subspecies or mixing of semispecies; blacked-in quadrants have negative endemism values for all endemic centers represented in their lists (i.e., more than half of the of the subspecies recorded and associated with any one center are present in populations hybridized with equivalent or conspecific taxa from other centers). Single crosshatching indicates endemism values above 1/3; double crosshatching indicates values over 2/3 of the corrected maximum for the center. (This maximum value is given after the name of each center; the number which follows in parentheses is the maximum if no correction for hybridization is applied.)

FIG. 14. Regions of high probability for the continuity of humid tropical forest during the long cold, dry spell which terminated the Würm-Wisconsin glaciation, 13,000–20,000 years ago (Brown, 1979, 1980). Areas were determined by a summation of separate data sets from paleoclimatological, pedological (soil characters), geomorphological (surface landforms), and vegetational analyses, including subtraction for especially unfavorable soils and vegetation types and a double positive value for especially favorable soils.

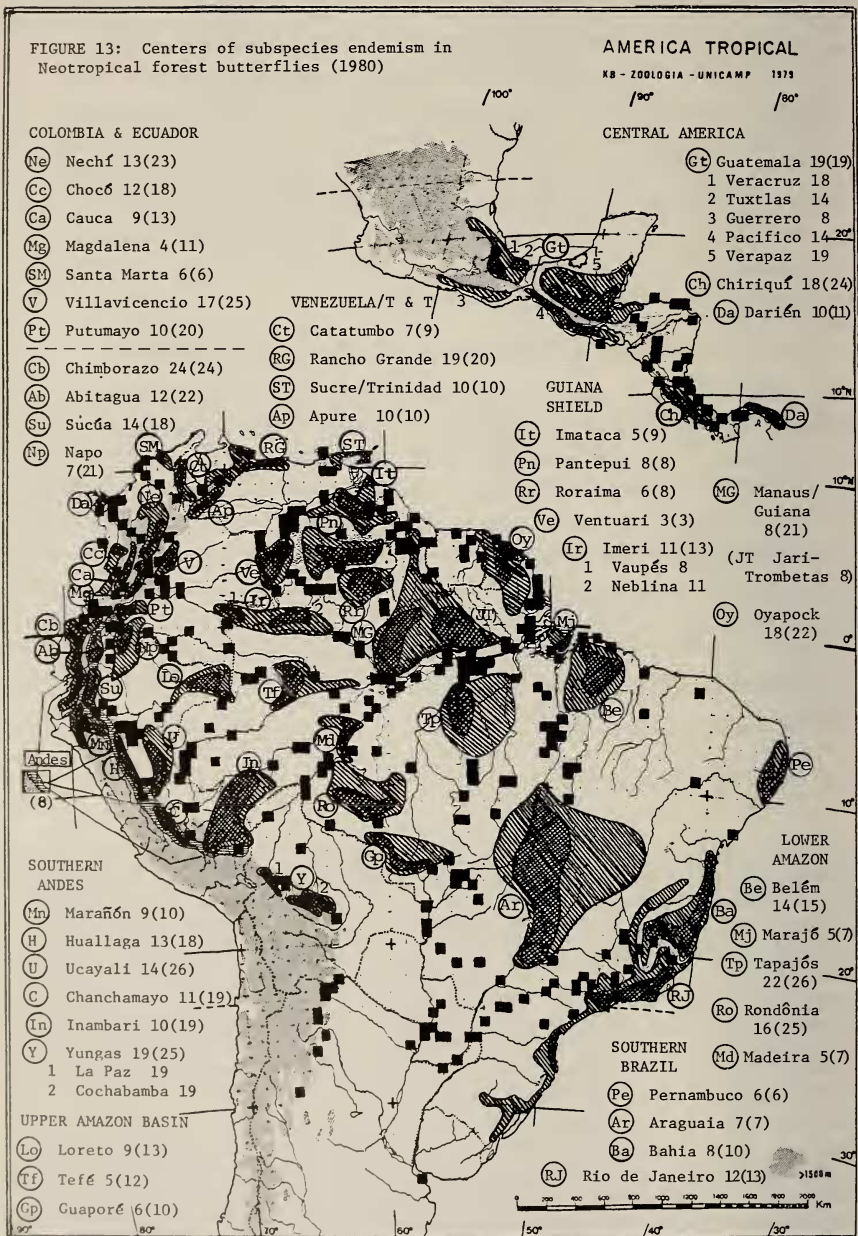


FIGURE 14: Paleocological Forest Refuges



SUGGESTED NAMES

AMERICA TROPICAL

KB - ZOOLOGIA - UNICAMP 1978

- 6 Nechí
- 7 Chocó
- 8 Chimborazo
- 9 Cauca
- 10 Magdalena
- 11 Santa Marta
- 12 Catatumbo
- 13 Rancho Grande
- 14 Sucre-Trinidad
- 15 Apure
- 16 Villavicencio
- 17 Putumayo
- 18 Napo
- 19 Abitagua-Baeza
- 29 Imataca
- 30 Cuchivero
- 31 Mucajá-Catrimani
- 32 Paríma
- 33 Huachamacari
- 34 Araçá
- 35 Neblina
- 36 São Gabriel
- 37 Vaupés
- 38 Apaporis
- 39 Guiana
- 40 Suriname
- 41 Oyapock
- 42 Serra do Navio

- 1 Guatemala (incl. Veracruz, Lacandona, Honduras)
- 2 Pacífico (incl. Guerrero, Socomusco, El Salvador)
- 3 Chiriquí-Azuero
- 4 San Blas
- 5 Tacarcuna

 60% PROBABILITY
 80-100% PROBABILITY

- 43 Jari-Trombetas
- 44 Manaus
- 45 Capim-Gurupi
- 46 Carajás
- 47 Tapajós-Xingú
- 48 Rondônia-Aripuanã
- 49 Purús
- 50 Juruá
- 51 Loreto-Japurá

- 20 Sucua
- 21 Marañón
- 22 Huallaga-Pachitea
- 23 Serra do Divisor
- 24 Chanchamayo
- 25 Inambari
- 26 Yungas
- 27 Uopiane
- 28 Guaporé

- 52 Ibiapaba
- 53 Cariris-Araripe
- 54 Pernambuco
- 55 Bahia
- 56 Agreste
- 57 Goiás
- 58 Pardo-Paraná
- 59 Paranapanema
- 60 Iguazu
- 61 Alegre
- 62 Rio de Janeiro



H. daphnis shows a characteristic pattern of distribution and abundance, in relation to the endemic centers (Fig. 13). The species appears uncommonly in restricted localities between the nuclei (regions with highest values for endemism) and the peripheries (regions where endemism values are positive but fall below 50% of the maximum) (Fig. 6). This suggests a partial marginalization process for the species, similar to but less accentuated than that in *H. leprieuri* (Fig. 8), which almost always occurs at the peripheries of endemic centers (endemism values near to 0). This distribution would maintain strong isolation between the subspecies of *daphnis*, but allow extensive hybridization in the subspecies of *leprieuri*.

The relationship of *H. daphnis* to *H. gemella* remains unresolved until more biological information is available. They are similar but not identical in male genitalia (Fig. 12); allopatric (Fig. 6); but they are not closely homologous in color-pattern elements. Together, they form a well-segregated subgroup within the genus *Hypothesis*.

Further discussion of speciation patterns in the genus *Hypothesis* and the biological distribution patterns of *H. leprieuri* and other species, as well as description of the many other new subspecies, must await additional fieldwork. Meanwhile, it is hoped that the species concepts presented here may be further tested in the field and in the laboratory, so that the genus may be better understood.

Hypothesis daphnis

Diagnosis. A *Hypothesis* characterized externally by the presence of a highly elongated submarginal spot in forewing space R_5-M_1 , contrasting with a small rounded spot directly above it in space R_4-R_5 ; and internally by male genitalia with a long thick penis and a fairly short and much narrower saccus, and three distinct teeth external to the tip of the valve. Sexes similar, with females having a larger wingspan, more rounded and opaque wings, and no hair-brush on the hindwing costa. Dorsal and ventral wing surfaces similar; abdomen yellow ventrally. Distributed in Brazil, from Amapá to Ron-

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FIGS. 15-21. *Hypothesis daphnis* adults (life size; dorsal left, ventral right; black, yellow and orange) and juveniles. **15**, *H. d. daphnis*, ♂ (a, upper) and ♀ (b, lower), Jaru, Rondônia (photos courtesy of Lee D. and Jacqueline Y. Miller of the Allyn Museum of Entomology); **16**, *H. d. daphnoides* ♂, km 185 Altamira a Itaituba, Pará, 13 Oct. 1977 (K. Brown); **17**, *H. d. madeira* nov., holotype ♂ (a, upper) and paratype ♀ (b, lower), km 519 Manaus-Porto Velho highway, Amazonas, Brazil, 17 Oct. 1978 (K. Brown); **18**, *H. d. clenchi* nov., holotype ♂ (a, upper) and allotype ♀ (b, lower), 27 km NE of Marabá, Pará, 8 Oct. 1977 (K. Brown). **19**, *H. d. amapaensis* nov., holotype ♂ (a, upper), allotype ♀ (b, center), and paratype ♂ with lighter forewing and darker hindwing (c, lower), Lourenço, Amapá, 30 June 1978 (K. Brown); **20**, *H. d. amapaensis*, mature larva, 2×, Lourenço, Amapá, green, whitish and ochre yellow; **21**, same, pupa, 3×, brown with reflections. Scale marks at left of figure indicate cm.



15



16



a



b

17



a



b

18



a



b



c

19



20



21

dônia; apparently absent west of the Rio Cuminá (Paru do Oeste, Erepecuru), north of the Solimões/Amazonas (where replaced by the congener *H. gemella*), and in the upper Amazon (where not substituted by any close species).

Key to subspecies

- 1a. Forewing median yellow patch broad, continuous from costal to anal margin, with postmedian yellow band narrow, broken into separate spots 2
- 1b. Forewing median and postmedian yellow bands nearly equal in width, separated by an irregular undulate black band 3
- 2a. Hindwing median black band narrow, margin with large yellow spots
..... *d. daphnoides*
- 2b. Hindwing median band broad or fused with all-dark margin *d. amapaensis* nov.
- 3a. Hindwing median band broken into four widely separated spots *d. madeira* nov.
- 3b. Hindwing median black band essentially continuous 4
- 4a. Forewing median black band jagged, postmedian yellow band narrow, often discontinuous; hindwing orange above a jagged black median band, with prominent yellow spots in the dark marginal area *d. daphnis*
- 4b. Forewing postmedian black band smoother, postmedian yellow band broad and continuous; hindwing orange above a smooth narrow median black band, no prominent yellow spots in narrow marginal black *d. clenchi* nov.

The distributions of the subspecies are shown in Fig. 6; all are illustrated in Figs. 15–19. Description of the three new subspecies follows notes on the two described previously by D'Almeida (1945).

Hypothesis daphnis daphnis D'Almeida, 1945 (Figs. 6 & 15)

Forewing (24–27 mm) with a jagged black band dividing the median-postmedian yellow region into two discontinuous crossbands of nearly equal width. **Hindwing** median black bar jagged but continuous; orange costally of this; marginal black including large yellow spots.

Distribution. Northwestern Mato Grosso, extreme southern Amazonas, most of Rondônia to extreme northern Bolivia (Guayeramerin). Registered localities and coordinates:

- Cidade Humboldt, Rio Aripuanã, Mato Grosso (10°13'S, 59°22'W)
- Mina Igarapé Preto, Amazonas (8°34'S, 61°10'W)
- Cachoeira do Samuel, Rio Jamari, Rondônia (8°45'S, 63°27'W)
- Rio Jamari, Rondônia (southwest of 9°S, 63°W)
- Porto Velho, Rio Madeira, Rondônia (8°45'S, 63°53'W)
- São Carlos, Rio Madeira, Rondônia (9°05'S, 64°05'W)
- 44 km N of Ariquemes, Rondônia (9°35'S, 63°03'W)
- 26 km SW of Ariquemes, Rondônia (10°04'S, 63°13'W)
- Porto Velho to Vilhena, km 260, Rondônia (10°18'S, 62°39'W)
- Jaru, Rondônia (10°27'S, 62°27'W)—very abundant in region
- Riozinho, Rondônia (11°30'S, 61°20'W)
- Jiparaná (Vila de Rondônia), Rondônia (10°52'S, 61°57'W)
- Guajara-Mirim/Guayeramerin, Rio Madeira, Rondônia/Bolivia (10°47'S, 65°20'W)

Hypothesis daphnis daphnoides D'Almeida, 1945 (Figs. 6 & 16)

Forewing (24–27 mm) crossed by a broad continuous yellow median patch and a narrow, broken postmedian spot-band. **Hindwing** black median band jagged, margin with large yellow spots.

Distribution. Area between the Xingu and Tapajós Rivers, Pará, Brazil, principally between 3° and 5° south latitude. Registered localities and coordinates:

22 km W of Belo Monte, Rio Xingu, Pará (Rodovia Transamazônica) (3°05'S, 51°52'W)
 Brasil Novo, km 35, Altamira a Itaituba, Pará (Rodovia Transamazônica) (3°18'S,
 52°33'W)

km 100, Altamira a Itaituba, Pará (3°29'S, 53°01'W)

km 124, Altamira a Itaituba, Pará (3°32'S, 53°11'W)

km 162, Altamira a Itaituba, Pará (3°39'S, 53°29'W)

km 185, Altamira a Itaituba, Pará (3°43'S, 53°44'W)

Rurópolis Presidente Médici, km 1552 Cuiabá-Santarém (junction with Rodovia Transamazônica), Pará (4°04'S, 54°56'W)

Igarapé Tinga, km 1557 Cuiabá-Santarém, Pará (4°01'S, 54°58'W)

km 190, Santarém a Rurópolis (km 1578 Cuiabá-Santarém), Pará (3°53'S, 54°54'W)

Monte Cristo, Rio Tapajós, Pará (4°05'S, 55°38'W)

Hypothyris daphnis madeira Brown new subspecies

(Figs. 6 & 17)

Forewing 25–29 mm (large for the species). Similar on the forewing to *H. d. daphnis*, but with the median black band smoothed to form a near-interrupted sinuate spot-band and a subtriangular cubital spot; black cell-spot large, rounded. **Hindwing** median black bar broken up into four separate oval spots.

Types: HOLOTYPE ♂, km 519 Manaus-Porto Velho highway, Amazonas, Brazil, ravine to west of road (6°31'S, 62°54'W), 17 Sept. 1978 (K. Brown), deposited in the Museu Nacional (Rio de Janeiro). ALLOTYPE ♀, Lago Acará, Rio Madeira, Amazonas, Brazil (southwest of 6°S, 62°W), Museu Nacional (Rio de Janeiro). One ♂ and 15 ♀ PARATYPES, same data as holotype; ♀ paratype distributed to each of the Museu Nacional (Rio de Janeiro), Departamento de Zoologia da Universidade Federal do Paraná (Curitiba), Museu Goeldi (Belém), Instituto Nacional de Pesquisas da Amazônia (Manaus), Allyn Museum of Entomology (Sarasota), American Museum of Natural History, National Museum of Natural History, Cornell University Collection, Carnegie Museum (Pittsburgh), Museum National d'Histoire Naturelle (Paris), Museum für Naturkunde (Berlin), and Zoologisches Sammlng des Bayerischen Staates (Munich); ♂ and 3 ♀ retained in author's collection. 3 ♂ and 5 ♀ PARATYPES, same data as holotype except collected by D. Gifford; one pair deposited in the British Museum (Natural History), ♀ in the Royal Scottish Museum (Edinburgh), 2 ♂ and 3 ♀ retained by D. Gifford, Brasília. One ♀ PARATYPE, "amont (below) Manaus," from Stoffel collection via H. Descimon, collection of the author.

Hypothyris daphnis clenchi Brown new subspecies

(Figs. 6 & 18)

Forewing (24–27 mm) not so heavily nor jaggedly marked with black as in *H. d. daphnis*, with a continuous and broad yellow postmedian band reducing the apical black area. **Hindwing** with median band smooth and narrow; marginal black also narrow with no yellow spots; disc translucent yellow in both sexes.

Types. HOLOTYPE ♂, 27 km NE of Marabá on highway PA-070, Pará, Brazil (5°11'S, 48°57'W), 8 Oct. 1977 (K. Brown), deposited in the Museu Nacional (Rio de Janeiro). ALLOTYPE ♀, Fazenda Terrasse, km 108, Açailândia-Santa Luzia road, Maranhão (4°24'S, 46°44'W), 2 Aug. 1974 (O. Mielke), in the Departamento de Zoologia, Universidade Federal do Paraná (Curitiba). 2 PARATYPE ♀, same data as holotype, retained in the author's collection. PARATYPE ♀, same data as allotype except 3 Aug. 1974, in the same collection (DZ-UFP). PARATYPE ♀, Água Azul, km 1490 Belém-Brasília highway, Município Paragominas, Pará, Brazil (4°20'S, 47°32'W), 16 Aug. 1974 (O. Mielke), also in the DZ-UFP. PARATYPE ♀, 33 km W of Paragominas (23 km E of large bend of the Rio Capim towards the west), Município de Paragominas, Pará

(2°58'S, 47°38'W), 5 Oct. 1977 (K. Brown), deposited in the Museu Goeldi (Belém). PARATYPE ♀, 30 km N of Marabá, Pará on PA-050 (5°03'S, 49°03'W), 8 Oct. 1977 (K. Brown), deposited in the British Museum (Natural History).

Hypothesis daphnis amapaensis Brown new subspecies
(Figs. 6 & 19)

Forewing (23–26 mm) similar to *H. d. daphnoides*, with a broad yellow median patch and four small postmedian spots. **Hindwing** much darker, the marginal black area without light spots, and the black median band heavy, occasionally fused to the marginal black.

Types. HOLOTYPE ♂ and ALLOTYPE ♀, Lourenço (Mines), Amapá, Brazil (2°19'N, 51°38'W), 29 June 1978 (K. Brown), donated to the Museu Nacional, Rio de Janeiro. 7 ♂ and 15 ♀ PARATYPES, same locality, 27 June to 1 July 1978 (K. Brown); one pair in each of the Museu Goeldi (Belém), the British Museum (Natural History), the American Museum of Natural History, and the Allyn Museum (Sarasota); ♀ in each of the Museu Nacional (Rio de Janeiro), Instituto Nacional de Pesquisas da Amazônia (Manaus), Departamento de Zoologia da Universidade Federal do Paraná (Curitiba), National Museum of Natural History (Washington), Cornell University collection (Ithaca), Carnegie Museum (Pittsburgh), Museum National d'Histoire Naturelle (Paris), Museum für Naturkunde (Berlin), and Zoologisches Sammlung des Bayerischen Staates (Munich); 3 ♂ and 2 ♀ retained in the author's collection. 3 ♀ PARATYPES, Utu, km 75 Calçoene-Lourenço, Amapá, Brazil (2°27'N, 51°24'W), 25–26 June 1978 (K. Brown), in the author's collection. ♀ PARATYPE, no locality (probably near Calçoene, Amapá), in the Museu Goeldi, Belém. ♂ PARATYPE, Tiriós, upper Rio Paru do Oeste (=Cumina), Pará, Brazil (2°14'N, 55°57'W), 29 Jan. 1975 (P. Bührnheim), in the author's collection.

Juvenile stages of *Hypothesis daphnis amapaensis*

During work in Lourenço, Amapá, in June 1978, I had occasion to observe two females of *H. daphnis amapaensis* ovipositing on plants of *Solanum asperum* L.-Cl. Rich.; one was a small bush on a field-and-stream edge (a typical habitat, where this plant is heavily attacked by *Hypothesis euclea* all over tropical Brazil), the other was a small tree in the middle of very dense forest above a small stream. A number of eggs and larvae in various stages were collected from these two plants. The larger larvae were reared to adults on the leaves of *S. asperum*, giving one male and one female (not paratypes). A brief summary of the early stages follows:

Egg subspherical (flattened where attached to leaf), glistening white, 0.5 mm in diameter, with numerous horizontal and vertical ridges, much as in the eggs of other solitary *Hypothesis* and many other Ithomiinae.

Larva (hatching after at least four days) initially translucent yellow, changing to greenish after feeding. First three instars (two to three days each) with few distinguishing marks other than the usual development of a "corrugated effect." They progress from rasping the underside of leaves to chewing at the edges.

Fourth instar larva similar to the fifth (Fig. 20). Mature larva near 30 mm in length; dorsally gray-green, supralaterally strong ochre yellow in a wide band. Semicircular lateral projections, one per segment, on the thorax and abdomen; each segment divided unequally in five "corrugations." Head and anal segment light greenish-white.

Total duration of larval feeding stage was about two weeks.

Prepupa doubled over in a "U" loop; whitish to yellowish. Duration one day.

Pupa (Fig. 21) brown, with some weak reflectiveness on wing-cases; strongly bowed

to assume the typical humped shape of many ithomiine pupae; eyes projecting in cones; wing cases and abdomen spotted with darker brown. Not nearly as silvered as most Dircennine pupae, but very similar to *Hypothyris ninonia*, *H. euclea*, and other *Hypothyris* pupae in shape and coloration. Duration eight days.

Adults emerge in the early morning, and fly before midday. They may then be found sparingly in the heavy, humid forest in steep ravines of the Serra Lombard around Lourenço Mines, where they fly all day long and are readily attracted to *Heliotropium* bait.

ACKNOWLEDGMENTS

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APPENDIX

Speciation and subspeciation in *Hypothyris* (Ithomiinae: Napeogenini)

The fundamental organization of the genus *Hypothyris*, based principally on male genitalia as employed in Fox & Real (1971), needs very little change. Fieldwork in hybridization zones has produced some unexpected indications of conspecificity of taxa maintained separate in that revision. A survey of the genitalia of most of the members

Note: Brown (1979) is available from the author to those who are studying the systematics and biogeography of Neotropical Lepidoptera. Mielke & Brown (1979) includes a taxonomic revision of the subfamily; it is available from either of the authors. Both include English summaries of the most important points.

of the genus (Fig. 12) also led to some surprises; not only did the genital armatures show appreciable variation within externally homogeneous populations, but also appreciably different genitalia were seen in patently conspecific taxa. For this reason, a biogeographical component was included along with the morphological parameters in the laying out of polytypic species (Figs. 2-11). Biological information from natural hybrid zones was employed whenever available; for example, it supported conspecificity of *H. vallina* and *H. pellucida* with *H. ninonia*, of *H. hygia* and *H. rowena* with *H. fluonia*, of *H. "aemilia"* and *H. fulminans* with *H. semifulva*, of *H. pyrippe* with *H. mamercus*, of *H. philetaera* and *H. laphria* with *H. euclea*, and of *H. honesta* with *H. anastasia*. Some of these unions were also supported by the biology of juvenile forms. In other cases, biological data confirmed the incompatibility of closely related species of similar morphology, such as *H. connexa* and *H. ninonia*, or *H. lycaste* and *H. anastasia*. Wide sympatry and strongly variant morphology suggested separate species status in the cases of *mansuetus* and *moebiusi*, *leprieuri* and *euclea*, and *valtonia* and *fluonia*. Many other decisions were educated guesses, based on a combination of morphology, biology, biogeography, and homology of minor color-pattern characters; for example, there is as yet no compelling biosystematic evidence for the association of *H. daeta* and *H. fimbria* with *H. ninonia* (although *diphes* seems secure there), of the Amazonian and Andean groups of subspecies of *H. mamercus* with each other, of *H. mayi* with *H. thea*, or of *H. glabra* with *H. lycaste*. The genitalia of *H. lycaste antonia* (Fig. 12) are very deviant within this species, and it may not be interfertile with *H. l. limosa*, though a recent common ancestry for the two seems very likely.

Examination of the respective types revealed that *Hypothyris glabra carvalhoi* (*sensu* Fox & Real) is in fact a subspecies of *Rhodussa cantobrica*, as originally described by D'Almeida. The very yellow, but ventrally orange-washed *ninonia* from north of the Roraima area (in Bolivar, Venezuela—Imataca center, Fig. 13) corresponds to *mysotis* (Haensch), differing from *colophonia* D'Almeida from south of Roraima in Brazil, and "*pellucida*," "*vallina*," and "*colosseros*" are transitions between these and neighboring subspecies (see Fig. 2). *Napeogenes seminigra* is in fact a subspecies of *Hypothyris fluonia* (and an older name for "*satterwhitei*" Fox & Real), as is the "problematic" *H. manausi*. *Maenas* is actually a transition between the extreme melanistic phenotype illustrated by Fox & Real (1971) and a new subspecies from lower elevations (Fig. 9); for the sake of stability this name should be applied to all orange-and-black populations from higher elevations in the Peruvian Andes. Weymer's *nemea* is an older name for Real's "*surinamensis*," but "*neustetteri*" and its senior synonym "*bifasciata*" are intergrades between *H. euclea philetaera* and *H. e. caldasensis*. The correct name for the Pernambuco subspecies of *H. ninonia* is *evanescens* Haensch or, if the original description be impugned for mistaken reference to an earlier name, is *evanescens* D'Almeida, 1923 (as a form) or 1939. Weymer's *daetina*, a dark chocolate form, must remain a *species inquerendum* until it is recaptured in Bahia. The oldest name for Riley's *medea* is *castanea* Butler (the male lectotype as designated by Mielke & Brown, 1979: 90, not the female illustrated by Butler = *a. anastasia*). The holotype designated by Haensch for his *latefasciata* is a senior synonym of *fugitiva* Fox, while Feisthamel's *leprieuri* (used with an extra "i" by Fox & Real for the Oyapock subspecies of *H. ninonia* = *H. n. latefasciata*) is actually the oldest named subspecies of the complex represented elsewhere by *ignorata*, *michaelisi*, *catilla*, *ninyas*, and a host of new subspecies (Fig. 8).

H. semifulva has two month's priority over "*aemilia*" for the species including both, which is fortunate because the latter name represents a rare transitional form between *H. s. angelina* and *H. s. pallisteri*.

The types of essentially all names have been seen. The majority of geographical subspecies recognized here (marked with an asterisk in Fig. 1) were studied in monomorphic populations in the field, in the appropriate regions. Names marked with a dagger on the list below were dissected to verify male genitalia, or slides prepared by Fox or Godman were examined in collections in the National Museum of Natural History or the British Museum, respectively.

Most specimens should be able to be rapidly identified with the drawings and geographical ranges shown in Figs. 2-11. In cases of doubt, the genitalia can be compared with those schematized in Fig. 12. The taxa which are most often confused on superficial characters are *ninonia/connexa* and *gemella/vollonia* in the Pantepui area, some *thealleprieuri* (note the different shape of the FW yellow median band, especially the distal border), *meterus/semifulva/anastasia* in the high Andes (genitalia work best), *ninonia/euclea/mamercus* in parts of the Amazon (the long narrow penis of the first can often be directly observed without a lens or dissection), *semifulva/mansuetus* in central Peruvian valleys (note the distal border of the FW yellow band), *leprieuri/euclea/ninonia* in various parts of the Amazon (compare the FW yellow fascia carefully), and *anastasia* with like species in the upper Amazon (the disjunct comma-mark in FW space Cu₁-Cu₂ will identify all *anastasia* subspecies).

At least ten, perhaps twenty more subspecies of *Hypothyris* should appear with intensive work in still little-explored parts of the Neotropics (in addition to the 31 already identified and still undescribed). Several of these, especially from the Marajó and Ventuari regions, are already in hand but awaiting broader field data and longer series to help decide on their status.

A list of the recognized specific and subspecific taxa follows, along with the association of each with an endemic center (Fig. 13) as used in the quantitative analysis of corrected endemism (Brown, 1979, 1980).

Genus HYPOTHYRIS Hübner, 1821

ninonia (see Fig. 2)

- †*granadensis* (Haensch, 1905) Magdalena(?)
- †*fimbria* (Hewitson, 1855) Villavicencio
- †*diphes* Fox, 1971 Putumayo
- †*latipennis* (Tessmann, 1928) Ucayali
(*antonina* Staudinger =
latipennis × *apollinis*)
- †manuscript subspecies (Brown) Inambari
- aetha* Fox & Real, 1971 Yungas
- †*cornelie* (Guérin-Ménéville, 1844) Guaporé
- †*mysotis* (Haensch, 1909) Imataca
- †*colophonina* D'Almeida, 1945 Roraima
- †manuscript subspecies (Brown) Pantepui
- †*completomaculata* (Zikán, 1941) Imeri
- †*mutilla* (Hewitson, 1867) Guiana
- †*completa* (Haensch, 1905) Manaus
- †*latefasciata* (Haensch, 1905) Oyapock
- †*ninonia* (Hübner, 1806) Belém
- †manuscript subspecies (Brown) Tapajós
- †*neimiyi* (Riley, 1931) Rondônia
- manuscript subspecies (Brown) Madeira
- manuscript subspecies (Brown) Tefé
- †*apollinis* (Staudinger, 1884) Loreto
- †*evanescens* (Haensch, 1909) Pernambuco
- †*daeta* (Boisduval, 1836) Rio de Janeiro
- meterus* (see Fig. 3)
- zephyrus* Fox, 1945 Putumayo
- †*meterus* (Hewitson, 1860) Andes
- deemae* Fox, 1943 Chanchamayo
- †manuscript subspecies (Lamas) Inambari
- connexa* (see Fig. 3)
- †*lema* Brown, 1977 Imataca
- †*connexa* (Hall, 1939) Pantepui
- †manuscript subspecies (Brown) Imeri

gemella (see Fig. 6)

- †*gemella* Fox, 1971 Imataca
- †manuscript subspecies (Brown) Pantepui
- †manuscript subspecies (Brown) Roraima
- daphnis* (see Fig. 6)
- amapaensis* Brown, 1980 Oyapock
- clenchi* Brown, 1980 Belém
- †*daphnoides* D'Almeida, 1945 Tapajós
- †*daphnis* D'Almeida, 1945 Rondônia
- madeira* Brown, 1980 Madeira
- fluonia* (see Fig. 4)
- †manuscript subspecies (Brown) Apure
- †*rowena* (Hewitson, 1857) Villavicencio
- berna* (Haensch, 1903) Napo
- uchiza* Lamas, 1979 Huallaga
- †*pardalina* (Hopffer, 1874) Ucayali
- seminigra* (Rosenberg & Talbot, 1914)
- †*viola* (Haensch, 1905) Inambari
- †*hygia* (Godman, 1899) Yungas
- manuscript subspecies (Brown) Oyapock
- †manuscript subspecies (Brown) Belém
- †manuscript subspecies (Brown) Tapajós
- †*manaos* (Bates, 1862) NW-Tapajós (Maués)
- tiberina* D'Almeida, 1945 Rondônia
- flavigera* (Riley, 1919) Madeira
- fluonia* (Hewitson, 1854) Tefé
- fulvifascia* (Talbot, 1932) Loreto
- †*violantilla* D'Almeida, 1952 Araguaia
- vollonia* (see Fig. 5)
- †manuscript subspecies (Brown) Roraima
- †*glycon* (Godman, 1899) Manaus/Guiana
- †*vollonia* (Hewitson, 1854) Belém
- †manuscript subspecies (Brown) Tapajós

Genus HYPOTHYRIS Hübner, 1821,
continued.

<i>semifulva</i> (see Fig. 5)		<i>leprieuri</i> (Feisthmel, 1835)	Oyapock
† <i>fulminans</i> (Butler, 1873)	Villavicencio	manuscript subspecies (Brown)	Belém
† <i>putumayoensis</i> Fox & Real, 1971	Putumayo	<i>ignorata</i> (Haensch, 1905)	Tapajós
† <i>satura</i> (Haensch, 1903)	Napo	manuscript subspecies (Brown)	Cachimbo (Tapajós—S)
† <i>semifulva</i> (Salvin, 1869)	Sucúa		Rondônia
† <i>pollisteri</i> Fox & Real, 1971	Huallaga	† <i>tinyas</i> D'Almeida, 1945	Rio de Janeiro
† <i>angelina</i> (Haensch, 1905)	Napo	†manuscript subspecies (Brown)	
† <i>meteroides</i> Fox, 1971	Andes		Guatemala
† <i>virgilini</i> (Riley, 1919)	Inambari	<i>euclea</i> (see Fig. 10)	Chiriquí
† <i>dalmeidai</i> Fox & Real, 1971	Rondônia	† <i>valora</i> (Haensch, 1909)	Darién
† <i>srora</i> (Srka, 1885)	Loreto	manuscript subspecies (Brown)	Nechí
<i>moebiusi</i> (see Fig. 7)		<i>leucanta</i> (Bates, 1863)	Chocó
† <i>moebiusi</i> (Haensch, 1903)	Napo	<i>philetaera</i> (Hewitson, 1876)	Rancho Grande
†manuscript subspecies (Lamas)		<i>caldasensis</i> Fox, 1971	Napo
† <i>unicolora</i> (Tessmann, 1928)	Huallaga	<i>euclea</i> (Godart, 1819)	Abitagua
<i>mansuetus</i> (see Fig. 6)	Ucayali	† <i>tintermedia</i> (Butler, 1873)	
† <i>amica</i> (Weymer, 1884)	Sucúa	<i>napona</i> (Haensch, 1903)	Huallaga
† <i>klotsi</i> Fox, 1941	Marañón	manuscript subspecies (Lamas)	Andes
† <i>mansuetus</i> (Hewitson, 1860)	Chanchamayo	<i>hemimelas</i> (Staudinger, 1885)	Ucayali
<i>mamercus</i> (see Fig. 9)		<i>pachiteae</i> (Tessmann, 1928)	Chanchamayo
† <i>polymnides</i> (Haensch, 1905)	Putumayo	<i>peruviana</i> (Staudinger, 1885)	Inambari
<i>mamercus</i> (Hewitson, 1869)	Napo	† <i>callanga</i> (Haensch, 1905)	Yungas
† <i>pyrippe</i> (Hopfler, 1874)	Sucúa	<i>nina</i> (Haensch, 1905)	Imataca
manuscript subspecies (Brown)		† <i>forbesi</i> Fox, 1941	Imeri
† <i>maenas</i> (Haensch, 1909)	Huallaga	<i>interrupta</i> (Zikán, 1941)	Belém
manuscript subspecies (Brown)	Andes	<i>barii</i> (Bates, 1862)	
† <i>poemne</i> D'Almeida, 1939	Guaporé	manuscript subspecies (Lamas)	Rondônia
†manuscript subspecies (Brown)	Manaus	† <i>laphria</i> (Doubleday, 1847)	Bahia
†manuscript subspecies (Brown)	Tapajós	<i>lycaste</i> (see Fig. 11)	
<i>thea</i> (see Fig. 3)	Rondônia	<i>dionaea</i> (Hewitson, 1854)	Guatemala
manuscript subspecies (Lamas)		† <i>callispila</i> (Bates, 1866)	Chiriquí
manuscript subspecies (Brown)	Ucayali	† <i>lycaste</i> (Fabricius, 1793)	Darién
† <i>thea</i> (Hewitson, 1852)	Inambari	† <i>limosa</i> Fox, 1971	Chocó
† <i>mayi</i> D'Almeida, 1945	Manaus	† <i>antonia</i> (Hewitson, 1869)	Chimborazo
	Altamira (Tapajós—NE)	<i>limpida</i> (Haensch, 1905)	Cauca
	Tapajós	<i>mergelena</i> (Hewitson, 1860)	Magdalena
<i>theatina</i> (Haensch, 1909)		† <i>fraterna</i> (Haensch, 1909)	Rancho Grande
<i>leprieuri</i> (see Fig. 8)		† <i>glabra</i> (Godman, 1899)	Villavicencio
manuscript subspecies (Lamas)		<i>anastasia</i> (see Fig. 11)	
manuscript subspecies (Brown)	Ucayali	† <i>honesta</i> (Weymer, 1884)	Putumayo
† <i>catilla</i> (Hewitson, 1875)	Inambari	<i>bicolora</i> (Haensch, 1903)	Andes
†manuscript subspecies (Brown)	Yungas	<i>anastasina</i> (Staudinger, 1885)	Ucayali
manuscript subspecies (Brown)	Guaporé	<i>acreana</i> D'Almeida, 1958	Inambari
† <i>nemea</i> (Weymer, 1899)	Roraima	<i>arpi</i> D'Almeida, 1958	Tapajós
† <i>nichaelisi</i> (Haensch, 1909)	Guiana	<i>niphias</i> D'Almeida, 1945	Rondônia
	Jari-Trombetas	<i>castanea</i> (Butler, 1877)	Madeira
		<i>anastasia</i> (Bates, 1862)	Tefé
		† <i>porsenna</i> (Srka, 1885)	Loreto